

## FEEDING BEHAVIOR AND FOOD HABITS OF WINTERING HARLEQUIN DUCKS AT SHEMA ISLAND, ALASKA

JULIAN B. FISCHER<sup>1,2,3</sup> AND CURTICE R. GRIFFIN<sup>1</sup>

**ABSTRACT.**—The foraging ecology of wintering Harlequin Ducks (*Histrionicus histrionicus*) is poorly understood and information on basic food habits is lacking for this species in the Aleutian Islands of Alaska where the largest winter concentrations occur. We investigated feeding behavior and food habits of wintering Harlequin Ducks in the western Aleutian Islands of Alaska with respect to sex and temporal and environmental variables to document behavioral responses to winter conditions, resource use, and nutritional requirements. We found that on average, Harlequin Ducks spent most of the diurnal period feeding (70% males, 76% females). However, more time was spent feeding during evenings, midwinter, cold weather, and high tides. Gastropods, crustaceans, and diptera larvae made up 83% of the diet, but diet composition changed throughout winter. Despite change in food habits, diet energy density was stable throughout winter. Received 29 Oct. 1999, accepted 5 March 2000.

Wintering waterfowl have evolved a broad range of feeding adaptations (Korschgen et al. 1988), but temporal and environmental factors influence the way they meet energetic requirements most efficiently (Paulus 1988). To understand foraging patterns in winter, researchers have investigated the response of waterfowl feeding behavior to time of day (Campbell 1978, Bergan et al. 1989, Paulus 1984), season (Paulus 1984, Rave and Baldassarre 1989), temperature (Nilsson 1970, Sayler and Afton 1981), and tide (Nilsson 1972, Petersen 1981). Such relationships help explain how waterfowl adapt to their local conditions.

Basic information on foraging ecology and food habits of Harlequin Ducks (*Histrionicus histrionicus*) is lacking in the Aleutian Islands of Alaska where the largest wintering populations occur (Bellrose 1976). Although winter time budgets and food habits were measured for Harlequin Ducks in Newfoundland (Goudie and Ankney 1986), intraspecific differences in feeding among wintering waterfowl suggest that the effects of temporal and environmental variables cannot be generalized throughout a species' range (Paulus 1988).

Temperate waterfowl in high northerly latitudes may have little flexibility in their feeding schedules because of fluctuating winter conditions (Thompson and Baldassarre 1991).

Therefore, information on the diurnal and seasonal foraging behavior of Harlequin Ducks may identify feeding periods crucial to the survival of this species in the Aleutian Islands. We investigated winter feeding behavior and food habits of Harlequin Ducks with respect to sex and temporal and environmental variables to document behavioral responses to winter conditions, resource use, and nutritional requirements.

### METHODS

**Study area.**—Shemya Island is located in the western Aleutian Islands of Alaska, approximately 2575 km southwest of Anchorage (52° 43' N, 174° 07' E; Fig. 1). Bounded by 22 km of shallow, rocky coastline, Shemya Island provides winter feeding habitat for approximately 500 Harlequin Ducks. Temperatures on site are moderated by the maritime climate, but high winds, fog, and snow are typical in winter months. Shemya Island is part of the Alaska Maritime National Wildlife Refuge and is currently leased to the U.S. Air Force. A coastal access road affords clear visibility of nearly the entire coastline and facilitates observational studies.

**Time budgets.**—We used the focal flock scan sampling method (Goudie and Ankney 1986, Baldassarre et al. 1988) to estimate Harlequin Duck diurnal time budgets at 6 coastal sites from December 1995 to March 1996 and November 1996 to January 1997. We used a stratified random process to select the time and location of observation sessions; therefore, each site was visited during each of 3 equal diurnal periods (morning, afternoon, evening) once every 3 days. To sample behavior from 30 min before sunrise to 30 min after sunset, we adjusted the start and end times of diurnal periods biweekly to compensate for seasonal changes in day length. We divided observations into three winter stages for analysis: early winter (1 Nov–20 Dec), midwinter (21 Dec–9 Feb), and late winter (10 Feb–1 Apr).

<sup>1</sup> Dept. of Forestry and Wildlife Management, Univ. of Massachusetts Amherst, Amherst, MA 01003-4210.

<sup>2</sup> Current address: U.S. Fish and Wildlife Service, Migratory Bird Management, 1011 E. Tudor Rd., Anchorage, AK 99503.

<sup>3</sup> Corresponding author:  
E-mail: julian.fischer@fws.gov



FIG. 1. Location of Shemya Island ( $52^{\circ} 43' \text{ N}$ ,  $174^{\circ} 07' \text{ E}$ ) in the western Aleutian Islands of Alaska.

We recorded behaviors of males and females separately in randomly selected focal flocks (one or more birds within 10 m of one another) every min during 1093 30-min sessions. If the focal flock separated into 2 or more groups, we continued observations on one randomly selected group. We employed switch sampling (Losito et al. 1989) when focal flocks were obscured for 2 consecutive scans. We categorized behaviors as feeding, locomotion, resting, preening, and other (flight, agonistic, pair bonding; Paulus 1988). When individuals did not dive or head-dip for more than 2 min, we recorded their behavior as resting. The proportion of time engaged in a behavior was estimated by dividing the sum of birds in each behavior category per session by the sum of birds in all categories per session (Goudie and Ankney 1986). Diurnal percent time spent feeding (percent time feeding) was calculated as the sum of dive, head-dip, and pause proportions. We estimated total diurnal hrs feeding/day by multiplying the proportion of day spent feeding by hr of daylight. We also recorded temperature and tide height before each 30 min observation session.

Accurately estimating time spent feeding by large flocks of diving ducks is problematic because of the difficulty in tallying submerged birds (Baldassarre et al. 1988). Most Harlequin Duck flocks at Shemya, however, were comprised of 1 or 2 birds and rarely more than 6 (Byrd et al. 1992, Meehan 1997) so we had little difficulty determining the proportion of diving birds in a flock during a scan.

We analyzed diurnal time budgets with parametric statistics after subjecting nonnormal percentage data to arcsine transformation (Zar 1984). We used the Shapiro-Wilk  $W$  test to confirm that behavior variables (percent time feeding, resting, in locomotion, and preening) satisfied the assumption of normality following data transformation ( $P > 0.05$ ). We used observation session as the sample unit to determine the relationship between dependent (behavior category) and independent (sex, diurnal time period, winter stage, temperature, tide, and day length) variables. We identified sex differences with independent  $t$ -tests and diurnal period and winter stage differences with ANOVA and Tukey's multiple comparison of means in a

randomized block design (observation sites = blocks). We then used correlation analysis to identify significant correlations between behavior and environmental variables (tide, temperature, day length). To determine if regression slopes differed by sex, we included sex as an indicator variable and tested for interaction effects between sex and environmental variables in each behavior category (Kleinbaum et al. 1988). All statistical calculations were performed on an IBM compatible personal computer using Stata 5.0 for Windows (StataCorp. 1997). Results are presented as means  $\pm$  SE.

**Food habits.**—To assess winter diet, we collected 43 actively feeding (observed  $>10$  min before shooting) Harlequin Ducks (22 male, 21 female) from December 1995 to March 1996 and November 1996 to March 1997. Immediately following collection, we removed all contents of the upper digestive tract (esophagus and proventriculus) and stored them in 70% ethyl alcohol (Swanson and Bartonek 1970). We used standard taxonomic keys to identify prey items (Bulycheva 1957, Gurjanova 1962, Pavlovskii 1966, Barnard 1969, Schultz 1969, Abbott 1974, Tsvetkova 1975, Fauchald 1977, Kozloff 1987) and estimated gross energy density ( $\text{kJ g}^{-1}$  dry weight) of esophageal and proventricular contents using published energy equivalents (Brawn et al. 1968, Cummins and Wuycheck 1971, Thayer et al. 1973, Reinecke and Owen 1980, Jorde and Owen 1988a). We limited our analysis to the upper digestive tract because differential digestion rates bias soft- and hard-bodied food items in the gizzard (Swanson and Bartonek 1970). We report aggregate percent dry mass (proportional mass of a given item in each bird averaged over all birds) and frequency of occurrence (birds with given food item/total birds; Bartonek and Hickey 1969, Swanson and Bartonek 1970, Swanson et al. 1974).

To analyze food habits we used the Wilcoxon rank-sum test and Kruskal-Wallis ANOVA to detect differences in each prey class by sex and winter period. We tested for differences in gross energy density of the diet by sex and seasonal period with parametric ANOVA.

## RESULTS

**Time budgets.**—Feeding behavior of Harlequin Ducks varied by sex and by temporal and environmental variables. Although both sexes fed during most of the diurnal period (Table 1), females spent more time feeding than males ( $t_{1091} = -5.46$ ,  $P < 0.001$ ; Fig. 2). In contrast, males spent more time than females in locomotion, resting, and preening ( $t_{1091} = 7.38$ ,  $P < 0.001$ ;  $t_{1091} = 4.00$ ,  $P < 0.001$ ;  $t_{1091} = 2.56$ ,  $P = 0.011$ ; Table 1).

Changes in Harlequin Duck feeding behavior were apparent among temporal variables. Both sexes concentrated feeding bouts in the evenings (male:  $F_{2,561} = 10.13$ ,  $P < 0.001$ ;



TABLE 1. Diurnal time budget of Harlequin Ducks at Shemya Island, Alaska, during winters 1995–1996 and 1996–1997.

| Sex    | Winter stage <sup>a</sup> | Diurnal period <sup>b</sup> | n <sup>c</sup> | % of time <sup>d,e</sup> |            |            |           |
|--------|---------------------------|-----------------------------|----------------|--------------------------|------------|------------|-----------|
|        |                           |                             |                | Feeding                  | Locomotion | Resting    | Preening  |
| Male   | Early                     | Morning                     | 64             | 63.7 (3.0) <sup>f</sup>  | 12.7 (1.5) | 18.7 (2.2) | 4.8 (1.0) |
|        |                           | Afternoon                   | 61             | 70.6 (3.0)               | 7.2 (1.0)  | 17.9 (2.2) | 4.0 (0.9) |
|        |                           | Evening                     | 64             | 79.5 (3.1)               | 7.4 (1.4)  | 10.5 (2.1) | 2.4 (0.6) |
|        | Mid                       | Morning                     | 63             | 76.4 (2.4)               | 8.7 (1.1)  | 11.7 (1.7) | 2.7 (0.6) |
|        |                           | Afternoon                   | 57             | 66.9 (3.7)               | 8.2 (1.1)  | 17.8 (2.6) | 6.2 (1.6) |
|        |                           | Evening                     | 53             | 79.5 (3.0)               | 6.1 (1.0)  | 11.7 (1.8) | 2.6 (0.5) |
|        | Late                      | Morning                     | 70             | 60.2 (3.2)               | 12.9 (1.4) | 20.9 (2.5) | 5.0 (0.7) |
|        |                           | Afternoon                   | 70             | 67.3 (2.9)               | 8.4 (0.9)  | 17.6 (2.0) | 6.4 (1.2) |
|        |                           | Evening                     | 69             | 69.5 (2.9)               | 8.3 (1.0)  | 16.7 (2.4) | 5.2 (0.8) |
| Female | Early                     | Morning                     | 57             | 77.4 (3.0)               | 6.2 (1.1)  | 12.3 (2.1) | 3.8 (1.2) |
|        |                           | Afternoon                   | 52             | 75.7 (3.8)               | 3.6 (0.8)  | 15.8 (2.7) | 4.4 (1.5) |
|        |                           | Evening                     | 55             | 79.9 (3.9)               | 5.1 (1.3)  | 9.8 (2.1)  | 4.8 (0.6) |
|        | Mid                       | Morning                     | 58             | 84.1 (2.6)               | 4.6 (0.7)  | 8.9 (2.0)  | 2.2 (0.6) |
|        |                           | Afternoon                   | 50             | 74.1 (4.4)               | 5.0 (1.0)  | 15.5 (3.1) | 5.2 (1.5) |
|        |                           | Evening                     | 55             | 87.4 (2.2)               | 3.6 (0.6)  | 7.2 (1.7)  | 1.8 (0.5) |
|        | Late                      | Morning                     | 69             | 70.7 (3.2)               | 9.0 (1.2)  | 15.3 (2.6) | 4.5 (0.9) |
|        |                           | Afternoon                   | 64             | 75.5 (2.9)               | 4.8 (0.7)  | 15.4 (2.4) | 3.9 (0.7) |
|        |                           | Evening                     | 62             | 74.5 (3.3)               | 5.8 (0.9)  | 14.8 (2.6) | 4.6 (1.0) |

<sup>a</sup> Early winter (1 Nov–20 Dec), midwinter (21 Dec–9 Feb), late winter (10 Feb–1 Apr).  
<sup>b</sup> Sampling occurred during three equal diurnal time periods from 30 min before sunrise to 30 min after sunset. The duration of these periods was adjusted biweekly to compensate for changes in day length.  
<sup>c</sup> Sample unit was each 30-min observation session.  
<sup>d</sup> Feeding, locomotion, resting, and preening accounted for >99% of diurnal activity.  
<sup>e</sup> Activity budget is reported as percentage of diurnal period.  
<sup>f</sup> SE in parentheses.

female:  $F_{2,512} = 3.71$ ,  $P = 0.025$ ; Table 1). As winter progressed percent time feeding increased and then decreased for both sexes (male:  $F_{2,561} = 7.56$ ,  $P < 0.001$ ; female:  $F_{2,512} = 8.78$ ,  $P < 0.001$ ; Fig. 2, Table 1). Despite a decrease in percent time feeding, total hrs

feeding/day increased in late winter (male:  $F_{2,561} = 24.35$ ,  $P < 0.001$ ; female:  $F_{2,512} = 32.33$ ,  $P < 0.001$ ), probably the result of a 72% increase in day length (Fig. 2).

Tide, temperature, and day length also were correlated with Harlequin Duck behavior. Behavior was not affected by tide direction ( $t_{1091} = 0.31$ ,  $P > 0.05$ ), but tide height was positively correlated with percent time feeding ( $F_{1,1091} = 18.77$ ,  $P < 0.001$ ) between both sexes equally (no interaction with sex;  $F_{1,1089} = 0.90$ ,  $P > 0.05$ ). Conversely, temperature was negatively correlated with percent time feeding ( $F_{1,1091} = 8.07$ ,  $P = 0.005$ ) between both sexes (no interaction with sex,  $F_{1,1089} = 2.68$ ,  $P > 0.05$ ). Day length, too, was negatively correlated with percent time feeding ( $F_{1,1087} = 60.69$ ,  $P < 0.001$ ) between both sexes (no interaction with sex,  $F_{1,1085} = 0.25$ ,  $P > 0.05$ ).

**Food habits.**—The winter diet of Harlequin Ducks consisted of 49 prey taxa from 10 classes (Table 2). Principal diet classes included gastropods (primarily *Littorina sitkana*), crustaceans (predominately gammerid amphi-

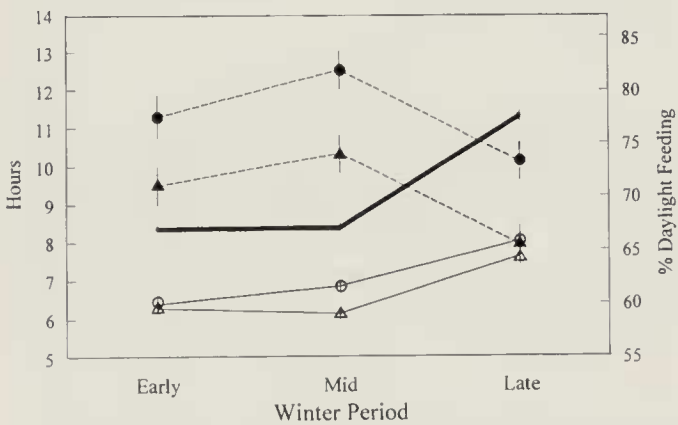


FIG. 2. Percentage of daylight time spent feeding (dashed lines) and total hr feeding (solid lines) relative to length of day (thick solid line) during three winter periods. Males and females are represented by triangles and circles, respectively. Error bars indicate  $\pm$  standard error.

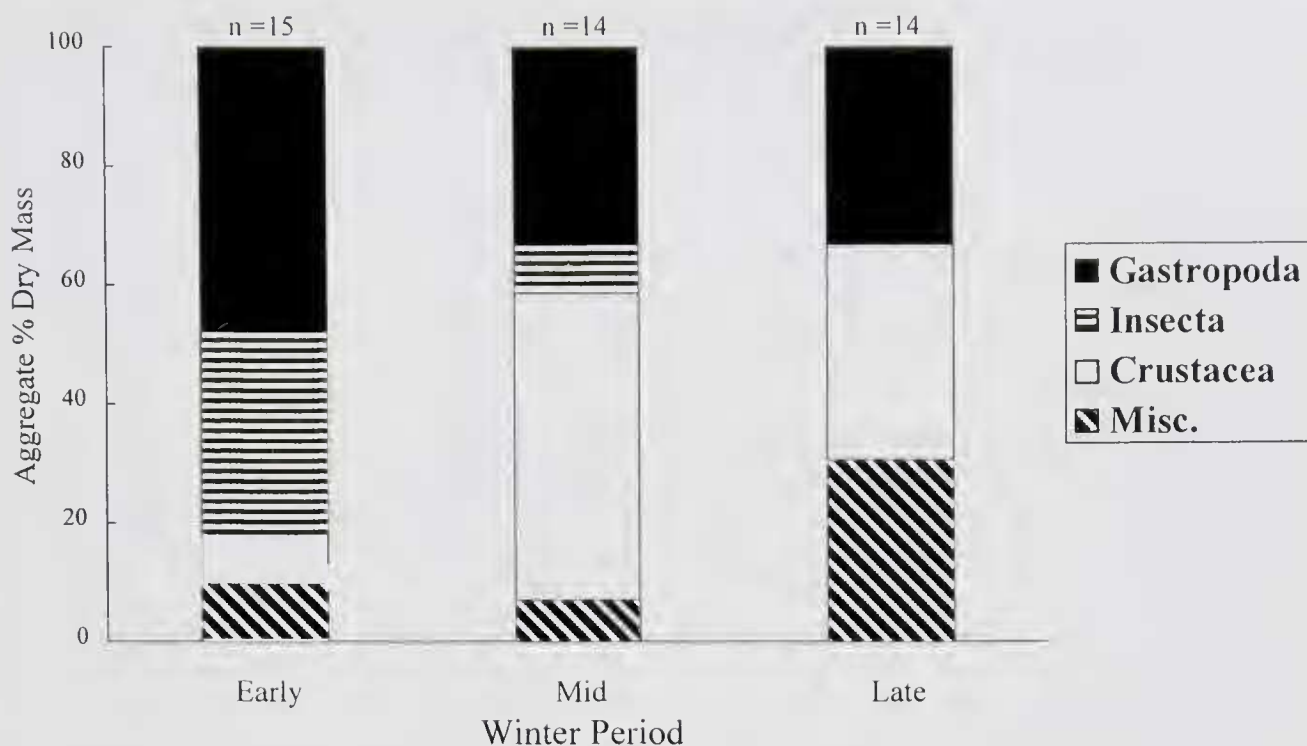


FIG. 3. Aggregate percent dry mass of diet classes identified from the upper digestive tracts of 43 Harlequin Ducks collected in winter at Shemya Island, Alaska, December 1995–March 1997.

pods), and dipterans (larvae and pupae), and did not vary between sexes ( $Z = -0.46$ ,  $P > 0.05$ ;  $Z = 0.62$ ,  $P > 0.05$ ;  $Z = -0.67$ ,  $P > 0.05$ , respectively). Similarly, gross energy density of the diet was  $11.38 (\pm 0.75)$  kJ g<sup>-1</sup> dry weight and did not differ by sex ( $F_{1,39} = 0.06$ ,  $P > 0.05$ ).

Food habits differed seasonally. Although consumption of crustaceans increased from early to midwinter ( $\chi^2_2 = 8.00$ ,  $P = 0.018$ ; Fig. 3), the opposite trend was detected for insect larvae ( $\chi^2_2 = 6.54$ ,  $P = 0.038$ ). Despite seasonal variation in the food habits of Harlequin Ducks, gross energy density of the diet did not differ between winter periods ( $F_{2,39} = 0.48$ ,  $P > 0.05$ ).

## DISCUSSION

Our investigation of wintering Harlequin Ducks revealed how diurnal time budgets and food habits varied by sex, time of day, season, and environmental conditions. Although females spent more time feeding than males, both sexes fed longer in the evening, in midwinter, at high tide, and during shorter days. In contrast, neither diet composition nor gross energy density of the diet varied by sex. Diets changed during winter but gross energy density of the diet remained constant.

Different foraging strategies by each sex may reflect energetic and physiological constraints. For example, differences in body mass of Harlequin Ducks at Shemya Island (male:  $750.9 \pm 9.7$  g,  $n = 22$ ; female:  $642.6 \pm 8.7$  g,  $n = 23$ ) could explain why females fed more than males. Although total energy requirements increase with body size, smaller birds have higher metabolic costs per unit body mass (Calder 1974). Moreover, the larger ratio of surface area to body mass among smaller birds leads to more rapid heat loss (Calder and King 1974); thus female Harlequin Ducks may have to accumulate fat reserves more rapidly during the day than males to compensate for greater fat loss at night (Kendeigh et al. 1977). In addition, female nutritional requirements may exceed those of males because of fat requirements before egg production (Bergan et al. 1989).

Seasonally, the decrease in percent time feeding in late winter was likely caused by lengthening day length. In late winter, when days are longer, diurnal feeding birds may be able to satisfy their energy requirements using a smaller percentage of daylight time because the days are longer (Kendeigh et al. 1977).

Tidal patterns also influenced feeding behavior. The timing of feeding bouts may de-

TABLE 2. Aggregate percent dry mass and percent occurrence of prey items in the upper digestive tracts of 43 wintering Harlequin Ducks collected while feeding at Shemya Island, Alaska, December 1995–March 1997.

| Species                                               | Aggregate % dry mass | % occurrence |
|-------------------------------------------------------|----------------------|--------------|
| <i>Buccinium baerii</i>                               | 2.16                 | 11.63        |
| <i>Neptunea</i> sp.                                   | 1.66                 | 4.65         |
| <i>Littorina sitkana</i>                              | 21.39                | 34.88        |
| <i>Littorina</i> sp.                                  | 2.57                 | 4.65         |
| <i>Lacuna</i> sp.                                     | 0.62                 | 11.63        |
| <i>Margarites albolineatus</i>                        | 2.33                 | 27.91        |
| <i>Cerithiopsis signa</i>                             | 0.05                 | 2.33         |
| <i>Volutidae</i> sp.                                  | 0.12                 | 2.33         |
| <i>Mytilus edulis</i>                                 | 0.18                 | 2.33         |
| <i>Tectura</i> sp.                                    | 1.73                 | 4.65         |
| <i>Lottia digitalis</i>                               | 0.54                 | 4.65         |
| <i>Lepidochitona</i> sp.                              | 0.07                 | 2.33         |
| <i>Tonicella</i> sp.                                  | 0.63                 | 2.33         |
| <i>Schizoplax brandtii</i>                            | 3.74                 | 27.91        |
| Total Gastropoda                                      | 37.79                | 67.44        |
| <i>Anisogammurus locustoides</i>                      | 6.50                 | 27.91        |
| <i>Anisogammurus pugittensis</i>                      | 3.34                 | 11.63        |
| <i>Paramoera</i> sp.                                  | 5.31                 | 20.93        |
| <i>Halirages bungei</i>                               | 0.30                 | 6.98         |
| <i>Melita</i> sp.                                     | 0.21                 | 6.98         |
| <i>Allorchestes malleolus</i>                         | 2.03                 | 6.98         |
| <i>Ampithoe</i> sp.                                   | 0.55                 | 9.30         |
| <i>Parhyale ochotensis</i>                            | 1.51                 | 6.98         |
| <i>Anonyx</i> sp.                                     | 1.42                 | 11.63        |
| <i>Pontogeneia</i> sp.                                | 1.89                 | 13.95        |
| <i>Gammaridea</i> sp.                                 | 0.76                 | 39.53        |
| <i>Idotea fewkesi</i>                                 | 0.19                 | 9.30         |
| <i>Exoshaeroma</i> sp.                                | 0.42                 | 6.98         |
| <i>Gnorimosphaeroma oregonensis</i>                   | 0.73                 | 13.95        |
| <i>Pentidotea wosnesenskii</i>                        | 1.18                 | 11.63        |
| <i>Pagurus aleuticus</i>                              | 1.30                 | 2.33         |
| <i>Heptacarpus brevirostris</i>                       | 0.12                 | 4.65         |
| <i>Hapalogaster grebnitzskii</i>                      | 0.36                 | 4.65         |
| <i>Pugettia gracilis</i>                              | 3.07                 | 9.30         |
| Total Crustacea                                       | 31.17                | 76.74        |
| Diptera pupae, <i>Brachycera</i> sp.                  | 0.44                 | 11.63        |
| Diptera larvae, <i>Muscidae</i> sp.                   | 13.72                | 13.95        |
| Total Insecta                                         | 14.16                | 25.58        |
| <i>Cucumaria</i> sp.                                  | 5.19                 | 23.26        |
| Total Holothuroidea                                   | 5.19                 | 23.26        |
| <i>Strongylocentrotus droebachiensis</i>              | 4.01                 | 16.28        |
| Total Echinoidea                                      | 4.01                 | 16.28        |
| <i>Ulothrix</i> sp.                                   | 3.70                 | 4.65         |
| Total Chlorophyta                                     | 3.70                 | 4.65         |
| <i>Nereis</i> sp.                                     | 0.37                 | 4.65         |
| <i>Teribellidae</i> sp.                               | 0.99                 | 2.33         |
| Polychaete sp.                                        | 0.67                 | 6.98         |
| Total Polychaeta                                      | 2.04                 | 13.90        |
| Fish eggs                                             | 0.41                 | 4.65         |
| <i>Cottidae</i> sp.                                   | 0.04                 | 2.33         |
| Perciformes ( <i>Stichaeidae</i> or <i>Pholidae</i> ) | 0.14                 | 2.33         |
| <i>Stichaeidae</i> sp.                                | 0.19                 | 2.33         |
| <i>Cyclopteridae</i> sp.                              | 0.10                 | 2.33         |



TABLE 2. CONTINUED

| Species                | Aggregate % dry mass | % occurrence |
|------------------------|----------------------|--------------|
| Total Osteichthyes     | 0.88                 | 11.63        |
| <i>Actinidae</i> sp.   | 0.62                 | 4.65         |
| Total Anthozoa         | 0.62                 | 4.65         |
| <i>Lepasterias</i> sp. | 0.16                 | 4.65         |
| <i>Asteroidea</i> sp.  | 0.28                 | 2.33         |
| Total Asteroidea       | 0.44                 | 6.98         |

pend on the way tide affects the availability of food (Jorde and Owen 1988b). Harlequin Ducks fed on intertidal and subtidal prey but never above the waterline, despite the fact that gastropods were accessible and exposed at low tide. This behavior may explain why feeding was positively correlated with tide level. If Harlequin Ducks choose prey submerged or at the water's surface, then food availability will increase with rising tide. This explanation is consistent with foraging theory predicting that in environments with fluctuating food abundance, birds are predicted to allocate the greatest time in habitats with high food abundance and less in areas of low abundance (Pyke et al. 1977).

Harlequin Ducks at Shemya Island apparently were generalists that maintained a stable energy balance by substituting fly larvae for crustaceans as winter progressed and supplementing their diet with diverse prey items. The Harlequin Duck winter diet elsewhere in its range includes many food types typically dominated by gastropods and crustaceans (Kenyon 1961, Vermeer 1983, Goudie and Ankney 1986, Gaines and Fitzner 1987). While insects are an important food on the breeding grounds (Bengtson 1972), there are no published reports that fly larvae occur in the diets of Harlequin Ducks elsewhere during winter; thus, consumption of fly larvae might be an adaptation to the Aleutian environment.

Although Harlequin Ducks may be adaptable in their food habits, our results suggest that they are constrained in the amount of time they must spend feeding during the winter. Behavior of Harlequin Ducks is most restricted during midwinter when they spent 80% and 87% of the evening feeding (males and females, respectively). Given the large amount of time spent feeding during midwinter, Harlequin Ducks would not be able to extend

their feeding bouts appreciably in the event of scarce food and/or cold temperatures. Future research should examine the susceptibility of Harlequin Ducks to winter starvation. Also, researchers should determine if Harlequin Ducks are able to feed at night during periods of cold weather and food scarcity, identify seasonal fluctuations in food quality and availability, and determine the energetic costs of specific behaviors.

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